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Use-Dependent Cortical Processing from Fingertips in Touchscreen Phone Users

Anne-Dominique Gindrat,[1,5] Magali Chytiris,[1,2,5] Myriam Balerna,[1,2,5] Eric M. Rouiller,[1] and Arko Ghosh[2,3,4,*]
[1]Domain of Physiology, Fribourg Cognition Center, Department of Medicine, University of Fribourg, Chemin du Musée 5, Fribourg 1700, Switzerland
[2]Institute of Neuroinformatics, University of Zurich and ETH Zurich, Winterthurerstrasse 190, Zurich 8057, Switzerland
[3]Neuroscience Center Zurich, University of Zurich and ETH Zurich, Winterthurerstrasse 190, Zurich 8057, Switzerland
[4]Institute of Cognitive Neuroscience, University College London, 17 Queen Square, London WC1N 3AR, UK

Summary

Cortical activity allotted to the tactile receptors on fingertips conforms to skilful use of the hand [1–3]. For instance, in string instrument players, the somatosensory cortical activity in response to touch on the little fingertip is larger than that in control subjects [1]. Such plasticity of the fingertip sensory representation is not limited to extraordinary skills and occurs in monkeys trained to repetitively grasp and release a handle as well [4]. Touchscreen phones also require repetitive finger movements, but whether and how the cortex conforms to this is unknown. By using electroencephalography (EEG), we measured the cortical potentials in response to mechanical touch on the thumb, index, and middle fingertips of touchscreen phone users and nonusers (owning only old-technology mobile phones). Although the thumb interacted predominantly with the screen, the potentials associated with the three fingertips were enhanced in touchscreen users compared to nonusers. Within the touchscreen users, the cortical potentials from the thumb and index fingertips were directly proportional to the intensity of use quantified with built-in battery logs. Remarkably, the thumb tip was sensitive to the day-to-day fluctuations in phone use: the shorter the time elapsed from an episode of intense phone use, the larger the cortical potential associated with it. Our results suggest that repetitive movements on the smooth touchscreen reshaped sensory processing from the hand and that the thumb representation was updated daily depending on its use. We propose that cortical sensory processing in the contemporary brain is continuously shaped by the use of personal digital technology.

Results

Cortical Fingertip Representations in Touchscreen Phone Users Differ from Those Found in Nonusers

We analyzed 37 right-handed volunteers, 26 of whom used touchscreen phones and 11 of whom used old-technology mobile phones. Questionnaires provided few key insights into how the more modern phones were used. First, touchscreen users primarily used their right thumb on the screen as opposed to other fingers (Figure 1A), and none of them used a stylus. The thumb preference was expected given that hand-held phones were designed as such [5]. Second, in agreement with a US national survey on smartphone use, 80% of the touchscreen users in our study mainly used their phone for receiving and sending text messages or e-mails, as opposed to passively listening to music, watching videos, or making calls [6]. Finally, according to the self-reports, touchscreen users spent noticeably more time with their phones than did the nonusers (Figure 1B).

We investigated whether the somatosensory cortical electrical activity evoked from the fingertips differed between touchscreen phone users and nonusers. Sixty-two surface electrodes distributed over the entire scalp were used to detect cortical potentials evoked by touch on the thumb, index, and middle fingertips of the right hand. Each tactile stimulus consisted of a light mechanical contact that lasted for 2 ms, and event-related potentials (ERPs) were based on 1,250 stimulations on each fingertip. For all three fingertips tested both in touchscreen users and nonusers, the touch resulted in a dipole field around the contralateral (to stimulation) somatosensory cortex with signal onset at 32 ms and peak at 55 ms (on grand mean traces). The positive ERPs were detected in the contralateral parietal electrodes, and the negative signals were detected more medially in the contra- and ipsilateral frontal electrodes (Figures 1C–1H). Based on the latency and signal topology, we could assert that these signals originated from the primary somatosensory cortex [7–9]. We analyzed the signal differences between the touchscreen users and nonusers across all time points (50 ms prestimulation to 120 ms poststimulation) and for each electrode by using two-sample t tests corrected for multiple comparisons using 2D spatiotemporal clustering [10]. Interestingly, for all of the tested fingertips, the amplitude of the positive ERP was larger in touchscreen users compared to nonusers (Figures 1C–1H). Temporally, the positive signals differed between 39 and 68 ms for the thumbtip, between 38 and 60 ms for the index fingertip, and between 48 and 66 ms for the middle fingertip (Figures 1C, 1E, and 1G). Spatially, the statistical maps revealed that the differences were clustered on the contralateral parietal scalp for all the three fingertips (Figures 1D, 1F, and 1H). However, the spatial extent of these differences was the smallest for the middle finger (Figure 1H).

In short, touchscreen users relied mostly on their thumb to interact with the screen, but the cortical potentials associated with the first three fingertips were enhanced in comparison to nonusers. However, the spatiotemporal impact of phone use was the least prominent for the middle fingertip.

The Amount of Touchscreen Phone Use Influences Cortical Activity

The increased cortical activity in touchscreen users compared to nonusers could be due to a more intense usage of the hand, in the sense that the former group used the right thumb more than the latter group did. Alternatively, it could be due to the development of touchscreen-specific motor routines or "skills" as the movements associated with push buttons (in nonusers, who used only old-technology mobile phones)

[5]Co-first author
*Correspondence: arko@ini.uzh.ch

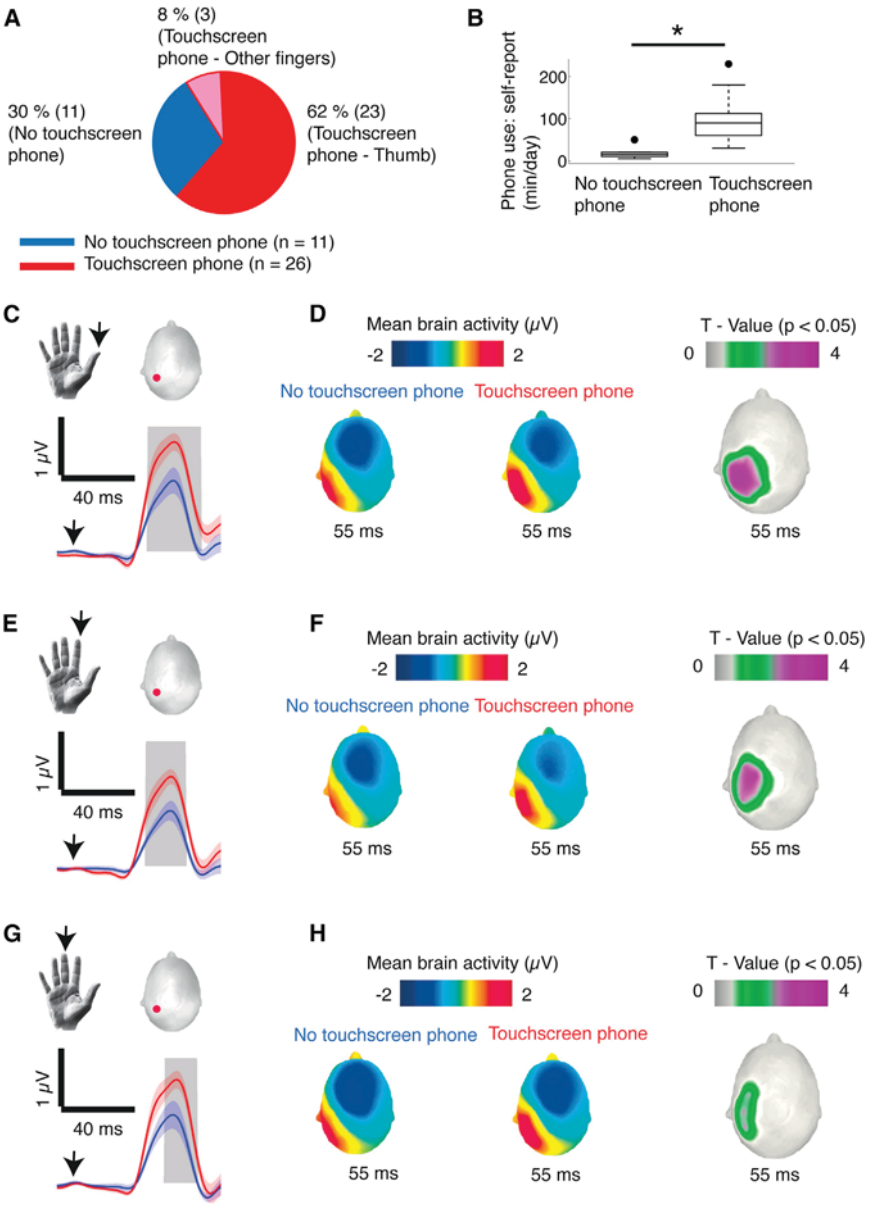

Figure 1. Tactile Event-Related Potentials in Touchscreen Phone Users and Nonusers

(A) Our study sample consisted of touchscreen phone users (red) and users of old-technology phones without touchscreens (blue), and most of the touchscreen users relied on their right thumb to interact with the screen (dark red).

(B) Box plot showing self-reported time spent using their mobile phone by touchscreen phone users and nonusers. Plot description: box, 25th and 75th percentile; whiskers, 10th and 90th percentile. Outliers are represented by black dots. *$p < 0.05$, Wilcoxon rank-sum test.

(C) Group means of the ERPs ± SEM (lighter shade) from the electrode with maximal positivity (red dot) in response to the right thumb tip stimulation in touchscreen users and nonusers. The gray area depicts significant differences between both groups—$p < 0.05$ and $T > 1$. The small arrow above the traces points at the stimulation onset (i.e., 0 ms).

(D) The corresponding scalp maps of the ERPs at 55 ms comparing the touchscreen users and nonusers. The multiple comparison corrected T value map revealed the electrodes with significant differences at 55 ms.

(E and F) Same as (C) and (D) but for right index fingertip.

(G and H) Same as (C) and (D) but for right middle fingertip.

versus taps or swipes on a smooth screen (in touchscreen phone users) were distinct.

To evaluate whether the cortical alterations scaled corresponding to touchscreen use, we identified three different attributes related to phone use: first, the self-reported age at which volunteers started using their touchscreen phone ("age of inception," Figure 2A). This attribute was inspired by previous reports on elite musicians and athletes in which the somatosensory representation of the corresponding body part was linked to the age at which practice began [1, 11]. Second, we quantified the history of phone use over a 10-day period by using built-in battery logs. Essentially, as the battery was drained with each phone use, the logs provided a proxy measure of finger-touchscreen interactions with a 10 min resolution, and the data were smoothed using a 50 min moving window [12]. The area under this curve was divided by the length of the recording period to derive the "phone use per hour"' (Figure 2B). Third, using the same smoothed battery signals, we estimated the time elapsed from a period of intense use—defined as the peak of battery drain—to the time of electroencephalogram (EEG) measurement ("duration from peak," Figure 2C; see also Figure S1 for scatter-plot matrix using the three variables). Based on preliminary simple linear regression between this measure and brain activity, we used the natural log of hours elapsed from the peak. Multiple regression analysis was conducted using these three phone use variables (Z′ normalized) for all time points (50 ms prestimulation to 120 ms poststimulation) and across all electrodes, resulting in event-related coefficients (ERCs) for each variable [10]. The regression statistics were corrected for multiple comparisons using 2D spatiotemporal clustering.

For the thumb tip, at the electrode with maximum mean positive ERP (grand mean of touchscreen user group), the corresponding "phone use per hour" ERC was also positive, and this linear relationship was significant between 33 and 44 ms and 53 and 61 ms (Figure 2D). Essentially, the higher the amount of phone use in the preceding 10 days, the larger the signal at the rising edge, peak, and falling edge of the positive ERP. At the electrode with the maximum mean negative ERP amplitude, the "duration from peak" ERC was significantly positive between 56 and 68 ms (Figure 2E). In other words, the longer the time elapsed from a period of intense use, the lesser the signal at the falling edge of the negative ERP. Scalp maps of the ERCs and the corresponding statistics captured the widespread impact of phone use (Figures 2F–2I). Overall, according to the R^2 value of the linear model, up to 60% of the interindividual variation in cortical activity could be

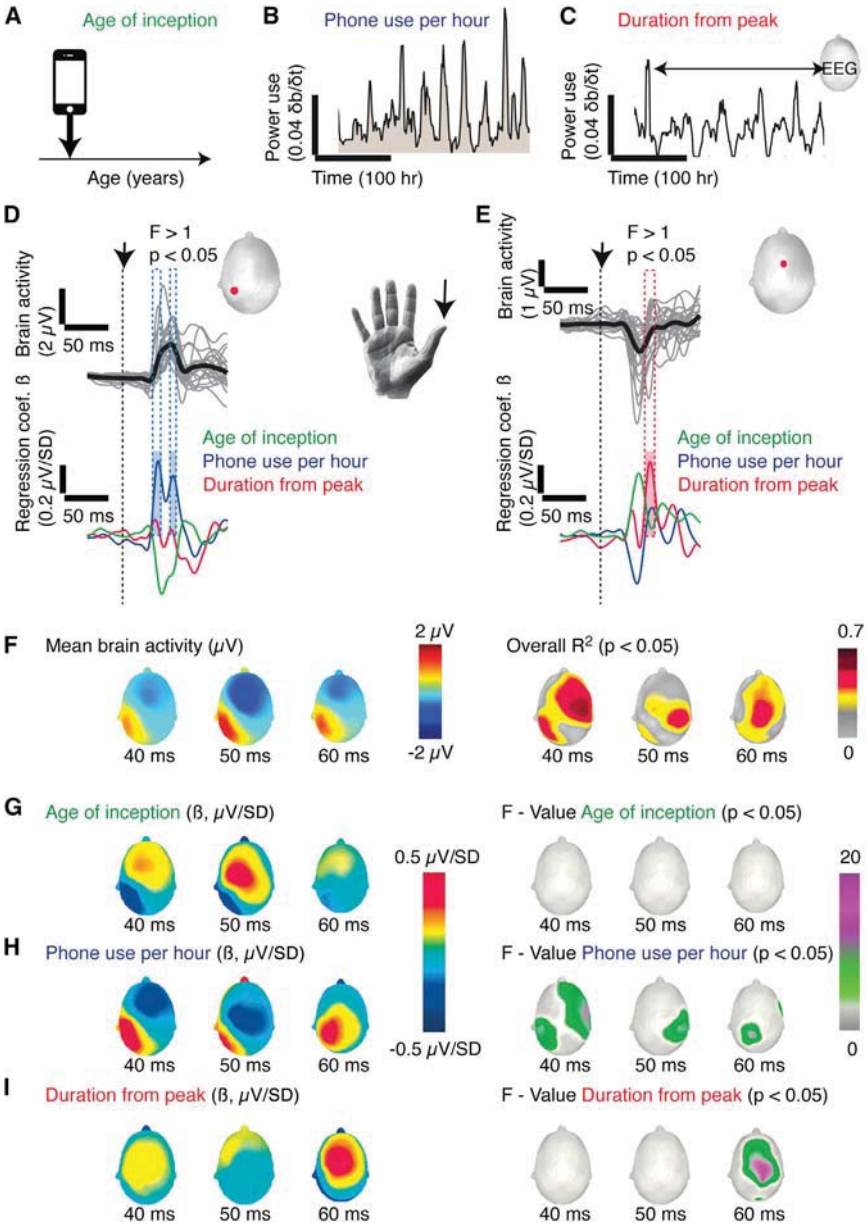

Figure 2. Interindividual Variations in Thumb ERPs Were Related to Touchscreen Phone Battery Logs

(A–C) To investigate how touchscreen use shaped cortical sensory processing, we identified three independent variables for multiregression analysis. We determined from the self-reports the age at which volunteers began using touchscreen phones ("age of inception," A). From the battery logs, we extracted the area under the curve to determine how much the phone was used in a 10-day period ("phone use per hour," B) and the "duration from peak" of use to EEG measurement expressed as natural log of hours (C). All the variables were Z′ normalized.

(D and E) The regression analysis of the right thumb tip ERPs resulted in a time series of β values or event-related coefficients (ERCs), and the β values at the positive peak ERP electrode (red dot; D) and the negative peak ERP electrode (red dot; E) are shown. Twenty-four individual positive and negative ERP traces are plotted with thin gray lines, and thick black lines depict the corresponding means. The areas in the dotted line boxes depict significant β values and are color coded according to the variable. The small arrow above the traces points at the stimulation onset (i.e., 0 ms).

(F) Scalp maps of the mean ERPs and the corresponding goodness-of-fit estimate of the full regression model (R^2) at three consecutive time points poststimulation.

(G–I) Scalp maps of the estimated β values and the corresponding F statistics for the three variables. Note that both "phone use per hour" and "duration from peak" variables were significantly related to the ERPs across several electrodes. See also Figures S1 and S2.

explained by the chosen variables (Figure 2F). Focusing on individual ERC scalp maps, for the "phone use per hour," the electrodes that detected positive ERP showed positive ERCs, and the negative ERP electrodes showed negative ERCs (Figure 2H). The pattern was distinct for "duration from peak"—here, only the negative ERP electrodes were related to the variable and the relationship was reversed, i.e., the negative ERP electrodes showed positive ERCs (Figure 2I). Although the spatiotemporal pattern of "age of inception" ERCs appeared to be converse to the "phone use per hour" ERCs, no significant relationship was found between this variable and brain activity (Figure 2G).

For the index fingertip, the linear relationships at the maximum positive and negative ERP electrodes were more restricted than for the thumb tip (Figures 3A and 3B). Essentially, a significant relationship was found between the "phone use per hour" variable and ERP, but only for the maximum positive electrode between 32 and 43 ms. Simply put, the more the phone was used over the 10 days preceding the EEG recording, the larger the signal on the rising edge of the positive ERP. According to the scalp maps, the positive ERP electrodes showed positive ERCs (Figure 3E). The rest of the variables did not show any significant relationship to brain activity (Figures 3D and 3F). Nevertheless, up to 54% of the variations were explained by the linear model (Figure 3C). For the middle fingertip, no significant ERCs were found, although the linear model explained up to 55% of the variation (see Figure S2).

In sum, the cortical potentials associated with the thumb and index fingertips reflected the touchscreen phone use history recorded by using the 10-day battery logs. The cortical activity evoked by touch to the thumb tip was directly proportional to the amount of phone use over the past 10 days and inversely proportional to the time elapsed from a period of intense use. The potential evoked by touch to the index fingertip was also related to the amount of use, albeit to a lesser extent and not related to the latter variable.

Interfingertip Inhibitory Interactions Are Not Eroded by the Touchscreen Phone Use

When neighboring fingertips are simultaneously stimulated, the magnitude of the ERP is smaller than the arithmetic sum of signals from the corresponding individual stimulations

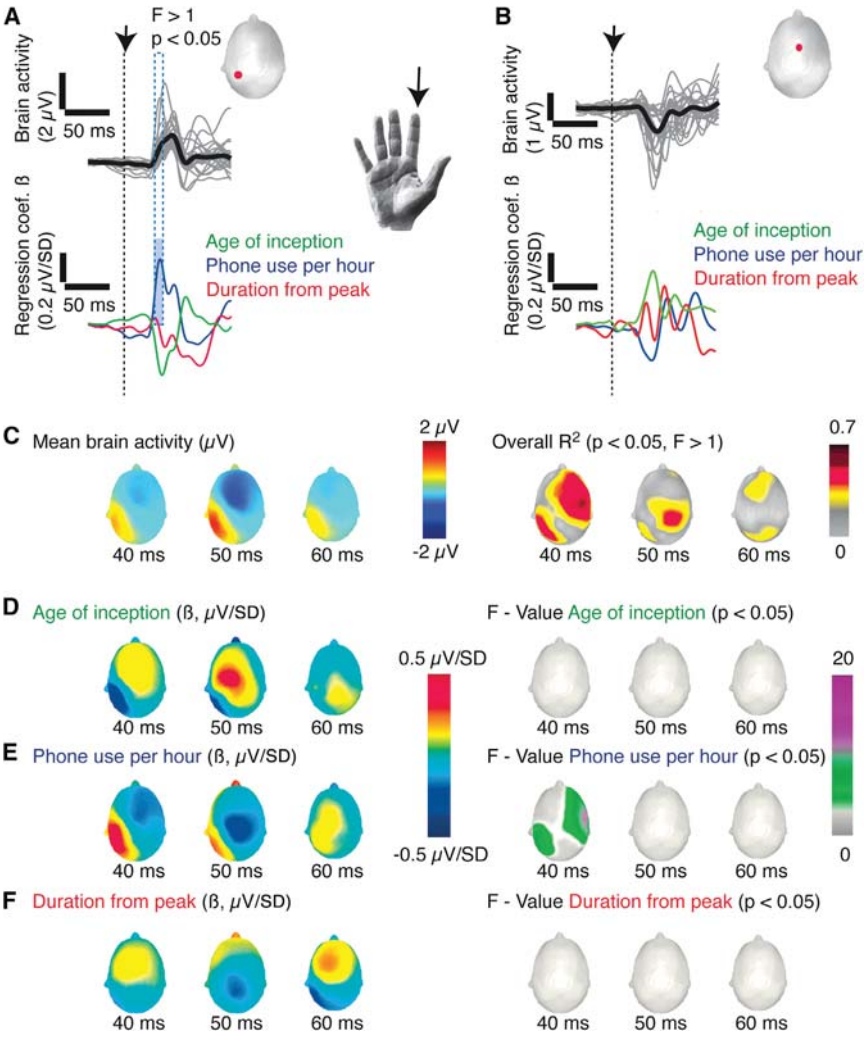

Figure 3. The "Phone Use per Hour" Variable Was Related to the Index Finger ERPs

The same variables as illustrated in Figure 2 for the thumb ERPs were used for regression analysis to model the index finger ERPs.

(A) At the positive peak ERP electrode, the area in the dotted line box depicts the significant β values or ERCs ("phone use per hour").

(B) No significant relations were found at the negative peak ERP electrode.

(C) Scalp map of the mean ERPs and the corresponding goodness-of-fit estimate of the full regression model (R^2).

(D–F) Scalp maps of individual β values and the corresponding F statistics. Note that only "phone use per hour" was significantly linked to the index finger ERPs.

The same conventions are used as in Figure 2. See also Figures S1 and S2.

poorly understood. Here, we found that the common use of touchscreen phones was associated with cortical reorganization. Touchscreen users showed larger amplitude of cortical potentials in response to tactile stimulation of the fingertips compared to nonusers. Furthermore, the amplitude was directly proportional to the recent phone use history quantified using battery logs built into the touchscreen phones. Intriguingly, transient cortical plasticity was induced within the monitoring period such that the thumb cortical potential was larger when volunteers' brain activity was measured soon after an episode of intense phone use than when measured later.

[13, 14]. This difference is theoretically explained by cortical lateral inhibitory interactions between the neighboring fingers. The increased cortical activity associated with individual fingertips in touchscreen users may have come at the cost of such inhibitory interactions. Essentially, unmasking the inhibition between the neighboring fingertips may have contributed to the larger potentials in touchscreen users [4, 15]. To address this issue, we measured the difference between the predicted and real ERPs in response to simultaneous stimulation of the thumb and index fingertips (Figure 4A). Touchscreen users were compared to nonusers using two-sample t tests across all electrodes and time points (50 ms prestimulation to 120 ms poststimulation) and were corrected for multiple comparisons using 2D spatiotemporal clustering. Interestingly, the proxy measure of inhibition was significantly enhanced in touchscreen users compared to the nonusers between 40 and 57 ms (Figures 4B and 4C).

Therefore, the increased cortical signals in touchscreen phone users were not associated with a loss of intracortical inhibitory activity.

Discussion

Plasticity of cortical tactile processing has been of intense interest, but how it is applied through our daily lives remains

The scalp recordings revealed positive and negative fields in response to fingertip stimulations, and yet the effects of touchscreen use were not always symmetric on either side of the putative dipole projection. First, for all fingertips, the positive ERP, but not the negative ERP, was significantly enhanced in touchscreen users compared to nonusers. Second, only the negative thumb tip ERP, not the positive one, was linked to the duration from the peak of use. It is important to note that the signal magnitudes were also asymmetric, i.e., the magnitude of the negative potential was 60% of the positive signal. Three factors were previously raised to explain this positive-negative magnitude asymmetry [16]. First, the volume conduction of the currents may be asymmetrically distorted due to the variations in the skull and head tissue. Nevertheless, this can be eliminated as an explanation of the touchscreen use-associated asymmetry, as these physical factors were unlikely to be systematically modified by phone use. Similarly, the curvature of the cortical surface could be eliminated as an explanation. The final and the most promising candidate is linked to the notion that EEG signals reflect a "spatial average" of several current dipoles [17, 18]. In theory, the scalp signals reflect a combination of tangential and radial dipoles. The former ones generate both positive and negative fields on the scalp, and the latter ones introduce a positive or negative component depending on their orientation. Indeed,

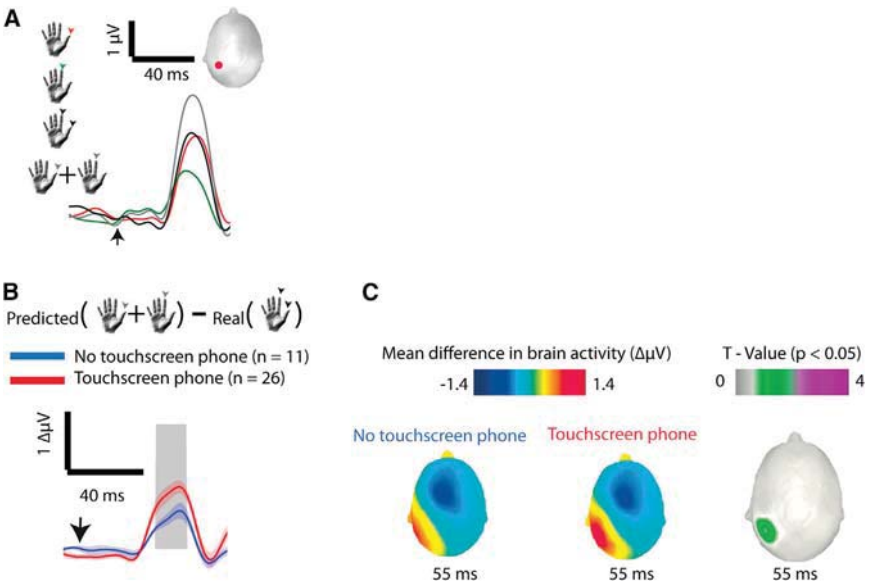

Figure 4. Sensory Integration from Thumb and Index Fingertips in Touchscreen Users and Nonusers

(A) An example measure from one volunteer depicting "inhibitory" interactions between the thumb and index fingertips. Note that the predicted (linear sum) signal magnitude (in gray) is larger than the real response evoked by simultaneous stimulations (in black).

(B) The difference between the predicted and real response magnitudes was enhanced in touchscreen phone users compared to nonusers.

(C) Scalp maps of voltage differences between the predicted and real response magnitudes in both groups and the corresponding T value map.

according to a combined EEG and magnetoencephalography (MEG) study, the primary somatosensory cortex (area 3b) generates both tangential and radial dipoles in response to electrical stimulation of the fingers [19]. Speculatively, the asymmetries described in our study may reflect touchscreen use-dependent alterations of the tangential as opposed to the radial sources. However, the exact neuronal origin of such a tangential source remains beyond the scope of our speculations, and isolating it would require a more improved theoretical understanding of how individual neurons in the somatosensory cortex contribute to the EEG signal at the scalp.

At first glance, the increased cortical activity in touchscreen phone users compared to nonusers appears to be similar to what occurs in string instrument players [1]. But a more detailed examination reveals two notable differences. First, the age at which musical practice began was strongly and linearly related to the cortical activity evoked from the little finger. However, this link between the age of inception and the cortical activity was not significant for touchscreen users. Furthermore, a daily diary of musical practice was maintained for a week, analogous to the 10-day battery logs used here. Whereas the musicians did not show any linear relationship to the recent activity, the touchscreen users did. Perhaps musicians enjoyed a more stable sensory representation than touchscreen users, shaped by disciplined practice through the early years. Notably, the minimum age of inception for musical practice was 5 years old, whereas for the touchscreen use it was 15 years old.

Based on the 10-day battery log versus brain activity correlations alone, it was not clear whether cortical processing was shaped by phone use over the past 10 days. Essentially, did the 10-day log reflect use over the past 10 days only, or was this log representative of use over a much longer period? For instance, the phone use levels may have remained stable over months and gradually shaped the cortical processing, but due to the stable usage the cortical signals may have still correlated well with the recent log. Based on previous studies, it appears that touchscreen use is at best "partially stable" [20, 21]. Among university students (studied here), several factors and their interactions may have contributed to unstable usage: as touchscreen phones are used toward educational activities, usage may have increased when approaching semester deadlines [21]. Intuitively, the usage levels varied with semester breaks as well. Intriguingly, moving from high school (where phones were generally disallowed) to university was also expected to alter how phones were used. Therefore, the 10-day log may have reflected past use on the scale of a few weeks but not years. Nevertheless, within the 10-day period of our study, phone use was uneven in each individual. Interestingly, cortical activity was significantly related to the day-to-day fluctuations, and this strongly suggested that the cortex was reshaped within this 10-day period. Essentially, volunteers who peaked their use a few days prior to the brain measurement had a larger thumb cortical potential than volunteers who had a longer gap between the peak of use and the brain measurement. Interestingly, previous laboratory experiments showed that 30 min of repeating simple taps with the thumb transiently reinforced motor cortical outputs [22]. Taken together, we speculate that both somatosensory and motor cortices conform to temporary increases in motor behavior by temporary reallocation of neuronal resources.

Although the rapidly transient cortical alterations were limited to the thumb, the cortical potentials from all the first three fingertips were enhanced in touchscreen users compared to nonusers. This suggests that the longer-term cortical alterations were not restricted to the skin surface most frequently used on the touchscreen (i.e., thumb fingertip). Kinematically, the index and middle fingers were involved in gripping and stabilizing the phone as the thumb hovered to touch the screen (data not shown) [23]. Therefore, the tactile receptors of the index and middle fingers tips were also activated during the phone use. Additionally, a less intuitive source of activations during phone use may have come from the tactile receptors on the hand, which are activated during grasping actions even without direct contact [24, 25]. Therefore, repetitive contact-based and contact-free coactivations of several receptors across the hand surface may have driven "hebbian-like" plasticity to increase the cortical potentials associated with all the fingertips [4, 26, 27]. However, this form of widespread plasticity was not triggered by the very short-term fluctuations in use, restricting the rapidly transient cortical alterations to the thumb tip only.

The mechanisms underlying cortical reorganization in touchscreen users remain unclear. The potential explanations are as follows: first, use-dependent increase in cortical activity has been previously associated with a recession of

intracortical inhibition [15, 28], but this was not found here with simultaneous stimulation of thumb and index fingertips. Still, as only the fingertips were tested, this mechanism cannot be entirely ruled out by our data. Second, touchscreen phone use may have strengthened the synapses in the somatosensory cortex, resulting in larger cortical potentials. This idea is supported by experiments involving brief periods of low-intensity direct-current stimulation of the cerebral cortex—which strengthens cortical synapses and increases the amplitude of somatosensory cortical potentials [29–32]. Third, the cortical alterations may be accompanied with subcortical alterations in touchscreen users. After amputation or spinal cord injury, nonhuman primates showed profound cortical changes, which were partly explained by the plasticity of the brainstem and thalamic circuits [33, 34]. Finally, we cannot entirely rule out peripheral modifications such as a decrease in threshold of the mechanical receptors driven by phone use, but such a use-dependent alteration of peripheral structures remains unreported in the neuroscientific literature. Furthermore, extensive research on experienced blind Braille readers provides strong evidence for central, but not peripheral, changes in people subjected to repeated tactile contacts with a fingertip [35, 36]. Nevertheless, according to dermatological research, "friction-induced dermatoses" may be observed in computer and mouse users, but only in case of severe usage (4–10 hr of daily use for 5–10 years), putatively resulting in the reduction of tactile inputs due to a build-up of extra layer of tissue over the damaged skin [37, 38]. Still, we cautiously speculate that a combination of central changes, rather than changes in the periphery, is more likely to be the underlying cause of the altered cortical potentials linked to touchscreen use.

In conclusion, touchscreen phone use reorganized the representation of the fingertips in the somatosensory cortex. The focus on regular touchscreen phone users complements the series of investigations already performed in elite athletes and musicians. Essentially, our study provided direct empirical insights into the operation of brain plasticity through our regular day-to-day activities, and this would not have been possible by studying expert groups or highly trained monkeys in a laboratory. Moreover, we unlocked a new method to nonintrusively quantify daily hand use by using battery logs, and this could be used to calibrate somatosensory potentials in basic and clinical neurophysiology. The consequences of the observed alterations may have been adaptive in the sense that they contributed to the development of useful associations between touch and phone activities. However, it is as likely that the plasticity was maladaptive. For instance, cortical plasticity in string instrument players is associated with dystonia [15, 39]. Furthermore, plasticity of the somatosensory cortex is associated with the development of chronic pain [40]. Worryingly, there is some evidence linking excessive phone use with motor dysfunctions and pain [41, 42]. More research is still needed to unravel the consequences of the altered sensory processing linked to the use of touchscreen devices.

Experimental Procedures

Volunteers

This study was conducted on 38 healthy right-handed mobile phone users between 19 and 34 years old (median: 22.9; 18 males and 20 females). Among them, 27 were touchscreen smartphone users (median: 22.9; 12 males and 15 females) and 11 were old-technology mobile phone users (median: 23.2; six males and five females). The volunteers, all university students, were recruited via mass e-mails and lecture hall announcements. By using self-reports, we eliminated hand injuries, history of neurological disorders, and medications that might have affected the nervous system. We also confirmed the volunteers' handedness using a questionnaire [43]. All volunteers were compensated for their participation with gift cards or course credits. One person (female touchscreen phone user) chose to drop out of the study by missing the brain measurement and was eliminated from all analyses. In this study, we considered a smartphone, as opposed to an old-technology mobile phone, to be any mobile phone with a fast processor and full front panel touchscreen, such as iPhone and Samsung Galaxy. Informed consent was obtained from all participants, and the Canton of Vaud approved the experimental procedures in accordance with the Swiss federal law on human experimentation.

Mobile Phone Use Survey and Battery Logs

All volunteers were probed on mobile phone use behavior via a questionnaire. This was used to extract the number of years the volunteers owned a touchscreen smartphone (i.e., leading to the age of inception) and/or an old-technology phone, to document the mobile phone model, to list any other personal digital technology owned, to estimate the time spent on the phone, and to specify the mode of interaction (stylus, voice, or touch). The questionnaire also included a list of 18 hand/finger postures on a touchscreen smartphone, and touchscreen phone users were instructed to rank them from the most-favored to the least-favored posture. Similarly, mobile phone activities were also ranked from a list of 11 actions that included text messaging and phone calls. Furthermore, the typing actions and grip style of all volunteers were also documented with a 480 fps camera.

We focused on battery logs from touchscreen phones to quantify use in a nonintrusive manner prior to the brain activity measurements over a period of 10 days. In one user, the data were available for 30 days due to rescheduling of a missed brain measurement session. However, such quantifications could not be performed with the old-technology (nontouchscreen) phones due to the lack of easy access to the battery sensors. All the touchscreen phones included in this study used similar batteries, with manufacturer's specifications on the battery life ranging from 6–8 hr of talk time on 3G, 10–14 hr of talk time on 2G, 4–7 hr of web use over 3G, and 7–10 hr of web use over Wi-Fi. The percentage of battery power was registered every 10 min when the phone was in use with the DataWiz app (Princeton EDGE Lab). The change in state of the battery over time was quantified using differences between consecutive samples (MATLAB R2011b). The negative differential indicated battery drain, and the positive differential indicated gain such as in charging of the phone. Because we were only interested in phone use, all positive values were set to 0, and remaining absolute values were used for further analysis. The data were smoothed using a 50 min moving window. The area under the differentials divided by the entire recording period (in hr) and the natural log of the time interval from the differential peak (from the entire recording period) to the time of brain measurement were extracted using MATLAB. The app malfunctioned in two volunteers due to users' error and the corresponding data were eliminated from further analysis.

Tactile Stimulations and EEG

The thumb, index, and middle fingertips of the right hand were randomly stimulated using solenoid tappers (Heijo Research Electronics), which could be precisely computer controlled in time via a stimulation box using a homemade script running on MATLAB. The tappers applied a 2-ms-long circular suprathreshold touch stimulus with an interstimulus interval of 750 ± 250 ms and made a 12.5 mm^2 contact with the fingertips. Stimulations were randomly delivered either individually to the three fingertips or simultaneously to the thumb and index fingertips. In order to cover the noise made by the tappers, we made a background white noise audible via headphones.

The EEG data were acquired from 62 electrodes mounted on an elastic cap (EasyCap) and distributed equidistantly to cover the entire scalp. Two additional electrodes were used for electro-oculogram (EOG) to monitor eye movements. The electrode locations were digitized in a 3D nasion-ear coordinate frame (ANT Neuro and Xensor software) for a representative volunteer. The EEG signals were recorded against the vertex and amplified with an alternating-current-coupled amplifier (BrainAmp, Brain Products). The data were sampled at 1,000 Hz, digitized using a 16 bit A/D converter, and rereferenced offline to the average signal from all the scalp electrodes (EEGLAB, an open source MATLAB toolbox [44]). The data were further analyzed with EEGLAB to band-pass filter between 1 and 80 Hz. All epochs that exceeded the ±70 μV threshold were eliminated to reject eye blinks from the analysis. Furthermore, trials containing statistically "abnormal" amplitudes were defined and eliminated using the kurtosis and joint

probabilities of the recordings (the threshold was set at 5 SD), and finally, eye movement artifacts and facial movement artifacts were rejected using independent component analysis (EEGLAB). ERPs for each stimulus location were obtained by averaging of 1,250 corresponding stimulations. Brain activity at each time point (−50 ms to 120 ms; 0 ms = stimulus onset; −50 to 0 ms = baseline) from each electrode and for each stimulus location was analyzed with a linear modeling approach. The two-sample t tests and multiple linear regressions (and the corresponding F tests) were corrected for multiple comparisons using 2D spatiotemporal clustering based on 1,000 bootstraps. All of the statistical and clustering analyses were conducted with LIMO EEG (MATLAB toolbox, using EEGLAB), and these tests are described here in detail [10].

Supplemental Information

Supplemental Information includes two figures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.11.026.

Author Contributions

A.-D.G., M.C., M.B., and A.G. collected the data and performed preliminary analysis. A.G. performed formal analysis and drafted the report, and A.-D.G., M.C., M.B., and E.M.R. edited its contents. A.G. provided the study concept, and A.-D.G., E.M.R., and A.G. designed the experiments.

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